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Decreased Precipitation Predictability Negatively Affects Population Growth through Differences in Adult Survival

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ABSTRACT: Global climate change is leading to decreased climatic predictability. Theoretical work indicates that changes in the climate's intrinsic predictability will affect population dynamics and extinction, but experimental evidence is scarce. Here, we experimentally tested whether differences in intrinsic precipitation predictability affect population dynamics of the European common lizard (*Zootoca vivipara*) by simulating more predictable (MP) and less predictable (LP) precipitation in 12 seminatural populations over 3 years and measuring different vital rates. A seasonal age-structured matrix model was parametrized to assess treatment effects on vital rates and asymptotic population growth (λ). There was a nonsignificant trend for survival being higher in MP than in LP precipitation, and no differences existed in reproductive rates. Small nonsignificant survival differences in adults explained changes in λ, and survival differences among age classes were in line with predictions from cohort resonance. As a result, λ was significantly higher in MP than in LP precipitation. This experimentally shows that small effects have major consequences on λ, that forecasted decreases in precipitation predictability are likely to exacerbate the current rate of population decline and extinction, and that stage-structured matrix models are required to unravel the aftermath of climate change.

Keywords: climate change, precipitation predictability, demography, seasonal age-structured matrix model, asymptotic population growth rate.

Introduction

The currently observed global climate change affects averages and variance of environmental conditions (e.g., average and variance of temperature) and decreases their temporal predictability (the degree of the temporal autocorrelation; IPCC 2013). These effects—but especially an environment's intrinsic predictability—may destabilize populations (Lindstrom and Kokko 2002) and increase their susceptibility to extinction (Lande 1993; Melbourne and Hastings 2008; Foden et al. 2009; Ashander et al. 2016). Changes in average environmental conditions have been largely studied, and nowadays it is clear that they are responsible for distributional shifts (Parmesan and Yohe 2003), local extinctions (Sinervo et al. 2010), species extinction (Huey et al. 2009; Lunney et al. 2014), and changes in biodiversity (Pounds et al. 2006). In contrast, much less evidence exists for responses to differences in environmental predictability (Gherardi and Sala 2015; Marshall and Burgess 2015), and controversy exists about the direction of the responses to differences in environmental variance (Lawson et al. 2015). Classic theory states that in less predictable environments, rapid and more frequent reproduction with minimal investment in offspring is favored (MacArthur 1984), and more recent theory states the contrary, that less predictable environments favor higher investment in individual offspring at the cost of litter size (Einum and Fleming 2004). Both theories suggest that an environment's intrinsic predictability may affect the trade-off between survival and reproduction and/or the trade-off between offspring number and quality (Stearns 1992; Einum and Fleming 2004; Nevoux et al. 2010), but they differ in the direction of the effect. Lack of robust evidence for either hypothesis compromises the understanding of how species respond to changes in environmental predictability, which is essential to predict effects of climate change on population dynamics, ecosystems, and biodiversity and for designing conservation measures (Ferrière et al. 2004; Saccheri and Hanski 2006; Kinnison and Hairston 2007; Chevin et al. 2013).

The few empirical studies (Dewar and Richard 2007; Marshall and Burgess 2015) suggest that decreasing environmental predictability may negatively affect vital rates, such as

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reproduction or survival. The effects of predictability on vital rates can elucidate whether and how species can deal with changes in environmental predictability, and they can be indicative for effects on population dynamics (Bjørnstad et al. 2004). However, frequently an effect's direction differs among different vital rates, and no significant differences and/or cohort resonance effects exist (Bjørnstad et al. 1999), requiring more sophisticated life-history analyses to understand whether and how population dynamics are affected (Bjørnstad et al. 1999; Layton-Matthews et al. 2018).

Here we experimentally test over three consecutive years whether and how differences in intrinsic precipitation predictability affect population dynamics using 12 independent seminatural common lizard *Zootoca vivipara* (Lichtenstein, 1823) populations. Half of the populations were exposed to more predictable (MP) and the other half to less predictable (LP) precipitation, with average precipitation held constant. Intrinsic precipitation predictability was manipulated, given the European common lizard's high dependency on water (Grenot et al. 1987; Lorenzon et al. 1999; Peñalver-Alcázar et al. 2016; Dupoué et al. 2017; Romero-Diaz et al. 2017) and given the changes in rainfall patterns observed in the past decades and predicted under climate change (IPCC 2013). Since in this species water availability constrains reproduction, litter size, and juvenile performance (Lorenzon et al. 1999; Bleu et al. 2013), different aspects of reproduction were measured and used together with individual vital rates to parametrize a seasonal age-structured matrix model for each predictability treatment based on the species-specific seasonal life cycle. Treatment effects on age- and season-specific vital rates and asymptotic population growth were tested and retrospective perturbation analysis were used to investigate which treatment effects (treatment effects on which age classes and seasons) mainly led to differences in asymptotic population growth (λ). These analyses thus allowed us to identify the key life-history processes that are most affected by changes in precipitation predictability and how they affect population dynamics, shedding light on how species may cope with changes in environmental predictability.

According to theoretic models (Tuljapurkar et al. 2009) and empirical studies (Dewar and Richard 2007; Marshall and Burgess 2015), we predicted (1) significant negative effects of LP precipitation on survival (Lawson et al. 2015; Ashander et al. 2016). In addition, we predicted (2) significant negative effects of LP precipitation on reproductive traits, such as laying success, hatching success, litter size, and newborn female ratio (Einum and Fleming 2004; Dewar and Richard 2007; Botero et al. 2015). Younger age classes are more affected by density-dependent effects and interage class competition than adults because of their lower competitive ability (San-Jose et al. 2016; Romero-Diaz et al. 2017). Hence, we predicted that (3) precipitation predictability may more strongly affect the competitively inferior age classes (namely, juveniles and yearlings) because of, for example, cohort resonance (Bjørnstad et al. 1999, 2004). As a result of the anticipated effects on vital rates, we also predicted (4) lower population growth in the LP environments.

Methodology

Study Species

The common lizard *Zootoca vivipara* (Lichtenstein, 1823) is a small ground-dwelling ovoviviparous lizard widely distributed throughout Eurasia. *Zootoca vivipara* inhabits humid meadows and grasslands, and humidity is a key predictor of habitat choice (Braña 1996; Peñalver-Alcázar et al. 2016). Humidity has been shown to affect individual activity, growth rate (Lorenzon et al. 1999, 2001), and several reproductive parameters (Lorenzon et al. 1999, 2001; Le Galliard et al. 2006, 2010; Bleu et al. 2013). Moreover, differences in the quantity of humidity and in its predictability are sources of intra- and interage variation in vital rates (Romero-Diaz et al. 2017).

Zootoca vivipara emerges from hibernation in March/April, and reproductive activities start just after the emergence of the females (Bauwens and Verheyen 1985; Fitze et al. 2010; Breedveld and Fitze 2015; fig. C1; figs. C1, C2 are available online). The reproductive system is polygynandrous (Fitze et al. 2005); in the oviparous populations, females lay one, two, and (in exceptional cases) three clutches per year, and average litter size is five, ranging between one and nine eggs (Heulin et al. 1994; Roig et al. 2000; Horváthová et al. 2013). In most populations, individuals attain sexual maturity in their second or third year of life (Horváthová et al. 2013; Roitberg et al. 2013), and the age of female maturity depends on body size and on the length of the activity season (Horváthová et al. 2013). In many populations, three age classes can be distinguished on the basis of body size and coloration (Pilorge 1987; Massot et al. 1992; Vercken et al. 2007): juveniles (first year of life), yearlings (second year), and adults (>2 years old). While juveniles and yearlings are generally immature, adults are mature and participate in reproductive activities. Almost all adult females produce eggs, and not all reproductively active males fertilize eggs (Fitze et al. 2010). In natural populations, survival ranges from 30% to 60% in adults (Heulin et al. 2011), 16% to 40% in immatures (Heulin et al. 2011), and considerably lower from 21% to 26% in juvenile lizards (Massot et al. 2011).

Seminatural Populations

All common lizards used for this experiment were originally captured from natural populations located in Aragón and Navarra, corresponding to the southwest European clade B (*Z. vivipara louislantzi*; Arribas 2009) and the northeast Spain subclade B4 (Milá et al. 2013; Horreo et al. 2018). Lizards were

individually marked by toe-clipping and kept in 12 semi-natural populations located at the Research Station El Boalar (Instituto Pirenaico de Ecología, Jaca; 42°33′ N, 0°37′ W, 700 m asl), consisting of enclosures (100 m^2) delimited by galvanized metal walls that were 1 m high and extended 1 m belowground to prevent the escape of lizards and the entrance of predators. To avoid predation, shrew traps were installed inside and outside the enclosures, and enclosures were covered by nets. Each population contained natural grassland, two water ponds, logs, and stone piles that provided lizards with naturally occurring prey, hiding, and basking sites (for more details, see Romero-Diaz et al. 2017). Prey was abundant, which is confirmed by higher adult survival compared with survival in natural populations (San-Jose et al. 2016; Romero-Diaz et al. 2017) and no significant treatment differences in body condition in any of the female age classes ($\chi^2 \leq 0.447$, $P \geq .504$).

In each experimental year, the same number of adults and yearlings and a similar number of juveniles were released in each enclosure (table 1). Average adult sex ratio at release (average: 35% males; table 1) corresponds to the average adult sex ratio of natural populations (average: 39% males; Le Galliard et al. 2005). No significant differences in the number ($F_{1, 10} = 1.033$, $P = .317$) and sex ratio ($F_{1, 10} = 0.005$, $P = .94$) of released juveniles existed among precipitation treatments (table 1). Lizards were randomly distributed among enclosures, and no significant differences existed among precipitation treatments in snout-vent length (SVL), body condition, and adult male color morph frequency (all $P \geq .2$). Adults and yearling lizards were released around mid-June (fig. C1), female lizards were released after parturition, and juvenile lizards were released 2 days after hatching. All lizards were released in unknown enclosures. Juveniles from the same clutch were released together in an enclosure different from their mothers' and not into the enclosure where the mother lived during the previous year. In each experimental year, all surviving lizards were captured in late spring. Half of the captured lizards—that is, half of each sex and half of each age class—were released in the same predictability treatment (but not in the enclosure in which they had been living before), while the other half was released in the other predictability treatment. Natural precipitation and temperature were assumed to be similar in all enclosures because they were located one next to the other in the same parcel of 2,000 m^2.

Precipitation Predictability Treatments

The intrinsic precipitation predictability was manipulated during 3 years using an automatic irrigation system. Each year, six populations were exposed to more and another six to LP precipitation by supplementing precipitation with four sprinklers per enclosure, one in each corner, which ensured homogeneous precipitation of the entire enclosure. In the MP treatment, two precipitation events happened every day (i.e., 14 supplemental precipitation events per 7 days), one at 0900 hours and the other one at 1800 hours, during the entire active period (mid-March to mid-October; fig. C1). Together with the natural precipitation, this treatment corresponded to MP precipitation events. In the LP treatment, the 14 supplemental precipitation events were randomly distributed among 7 days between 0900 and 1800 hours. Weighted permutation entropy of all obtained precipitation (natural plus experimental precipitation) was calculated to quantify the predictability of precipitation in each treatment level. Permutation entropy was larger in the LP treatment (0.86) and smaller in the MP treatment (0.77), showing that precipitation was less predictable in the LP treatment. Consequently, all enclosures obtained the same amount of precipitation, and the precipitation predictability significantly differed among precipitation treatments, but the variance in precipitation did not.

Weighted permutation entropy was calculated to quantify the intrinsic predictability of precipitation in each treatment level. Permutation entropy is a measure of time series complexity that is inversely related to predictability. Time series with high permutation entropy have low redundancy and low predictability (Garland and Bradley 2015). Weighted permutation entropy was calculated for each precipitation predictability treatment and year on the basis of the obtained daily amount of precipitation (natural precipitation plus supplemental precipitation) during the lizards' active season (from March to October). To calculate the permutation entropy, time series were translated into permutation patterns of length n (Riedl et al. 2013). Weighted permutation entropy was then calculated according to

$$H_n = \frac{-\sum_{j=1}^{n!} p_j \log_2(p_j)}{\log_2(n!)},$$

where p_j represents the relative frequencies of the observed permutation pattern (Bandt and Pompe 2002). The number of successive measures (n) included in a permutation pattern depends on the time series length (for more details, see Pennekamp et al. 2019), and $n = 4$ was optimal for our data set.

Data Collection

Survival. After release, two capture-recapture sessions were conducted, one at the end of August and the other one at the end of September (fig. C1). Each capture session consisted of three consecutive days of intensive capture with equal effort across time and enclosures. Captured lizards were individually identified and released on the same day and in the same enclosure where they were captured. Approximately at the end of May, all surviving lizards were recaptured (fig. C1) and brought to the laboratory, where they were kept in individual terrariums until release into the enclosures. Recapture of all

Table 1: Number of adults, adult sex ratio, number of yearlings, and number of juvenile lizards released per each enclosure and year

	Adults				Yearlings			Juveniles			
	Males	Females	Total	Adult sex ratio	Males	Females	Total	Males	Females	Total	Total
2012	7	13	20	.35	6	6	12	18.75 ± 1.06	9.67 ± 1.30	28.42 ± .79	60.4 ± .79
2013	10	17	27	.37	2	2	4	14.83 ± 1.9	5.67 ± 1.67	20.5 ± 1.57	51.5 ± 1.57
2014	9	18	27	.33	2	2	4	15.25 ± 2.14	6.83 ± 2.12	22.08 ± 1.44	53.08 ± 1.44
Mean ± SE	8.7 ± .9	16 ± 1.5	24.7 ± 2.3	.35 ± .0	3.3 ± 1.3	3.3 ± 1.3	6.6 ± 2.7	16.28 ± 1.2	7.39 ± 1.2	23.7 ± 2.4	54.99 ± 2.7

Note: The average number of lizards released per year and enclosure are given as well. Means ± SE are given where indicated.

surviving individuals was assured by searching a given enclosure for lizards until 5 days passed since the last lizard has been detected and recaptured in this enclosure. Survival was determined per capture session and corresponds to the recapture of a lizard on at least one of the three capture days (per session), following a robust design (Kendall et al. 1995).

Reproduction. From the end of April until the end of May (for first clutches) and from mid-June onward until mid-July (for second clutches; fig. C1), females were captured weekly and gravidity was determined by means of belly palpation. Gravid females were moved to the laboratory, where they were kept in individual terrariums under standardized conditions, while nongravid females and females with small eggs were released in the exact capture location directly after capture (fig. C1). All lizards that were brought to the laboratory were maintained in individual terraria that contained peat substrate, a hide, a water pond, and a heat source, and they were exposed to a standardized light regime (see San-Jose et al. 2016; Romero-Diaz et al. 2017). Lizards had access to water ad lib. and were fed every fourth day with wax moths (*Galleria mellonella*) or house crickets (*Acheta domesticus*). Every week, body mass was measured, individuals were checked for ectoparasites, and terraria were checked for mold and feces and replaced with a new one when necessary. Terraria of gravid females were checked twice a day for laid clutches. Litter size (i.e., the number of eggs) and laying date of detected clutches were recorded, and detected clutches were individually incubated in a constantly humid atmosphere at 21°C during the day (from 0900 to 2100 hours) and 19°C during the night (Heulin et al. 1997). Incubating eggs were checked daily, and sterile eggs or eggs containing dead embryos were removed. Once juveniles hatched, the number of juveniles hatched per clutch and the date of hatching were recorded. Juvenile lizards born before the August capture session were classified as early juveniles, and juveniles born afterward were classified as late juveniles, with the former corresponding to first clutches and the latter to second clutches. Data underlying the hereafter described models have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.349sn3f; Masó et al. 2019).

Seasonal Life Cycle

We developed a flexible seasonal life cycle for the southwest European common lizard *Z. vivipara louislantzi* (fig. C2), which allows testing how differences in age at first reproduction affect asymptotic population growth rate. The life cycle consists of three seasons that correspond to the oviparous common lizard's main life stages and to the time between capture sessions: May–August, August–September, and September–May (fig. C1), hereafter referred to as spring, summer, and winter for simplicity. Five life-history stages were considered: early juveniles (J_E), late juveniles (J_L), yearlings (Y), first-year adults (AD1), and adult lizards (AD). The life cycle was based on females because females represent the reproductive segment of the population (Caswell 1989). Survival and reproductive rates were calculated for spring and summer, and survival was calculated for winter. The life cycle valid for most *Z. vivipara* populations (Pilorge 1982; Heulin 1985; Massot et al. 1992) included the following stage- and season-specific vital rates: spring (sp): survival (S_{AD_sp}, S_{AD1_sp}, S_{Y_sp}), reproductive rate (R_{AD_sp}, R_{AD1_sp}); summer (sm): survival (S_{AD_sm}, S_{AD1_sm}, S_{Y_sm}, S_{JE_sm}), reproductive rate (R_{AD_sm}, R_{AD1_sm}); and winter (wt): survival (S_{AD_wt}, S_{AD1_wt}, S_{Y_wt}, S_{JE_wt}, S_{JL_wt}). The transition between age classes took place during winter: first-year adults (AD1), yearlings (Y), and juveniles (early and late juveniles) changed to the AD, AD1, and Y stages, respectively. Since in most populations lizards are not mature in the year following birth (Bauwens and Verheyen 1985), reproductive rates for adults and first-year adults (R_{AD}, R_{AD1}) but not for yearlings were calculated using several multiplicative fitness proxies:

$$R_a = L_a \times N_a \times H_a \times F_a.$$

These proxies consisted of laying success (L; 0 = no eggs laid, 1 = eggs laid), litter size (number of eggs; N), hatching success (H; $N_{\text{hatched offspring}}/N$), and female ratio of a clutch (F; $N_{\text{females}}/N_{\text{eggs}}$). The term a represents the age class and has two levels (AD and AD1) for the modeled basic life cycle (fig. C2).

Estimation of Vital Rates

All vital rates (survival and reproductive parameters) shown in figure C2, and those used for calculating R_a were estimated for each precipitation predictability treatment, age class, and season, using generalized linear mixed models (glmer or lmer from package lme4; Bates et al. 2015). Age class, treatment, and season were modeled as fixed factors, and enclosure, year, and individual identification (when appropriate) were modeled as random factors. We used glmer with binomial error distribution and a logit link for survival, laying success, hatching success, and female ratio (Bolker et al. 2009). For litter size, we used glmer with Poisson error distribution and a log link, and we used lmer with Gaussian error distribution for the other variables. To predict the mean and standard error of each vital rate from the fitted generalized linear mixed model, the function predictSE included in the package AICcmodavg (Mazerolle and Mazerolle 2017) was used. To test whether significant differences between precipitation predictability treatments existed in the vital rates, a permutation test was run at the enclosure level. To this end, all permutations for six enclosures with LP precipitation and six enclosures with MP precipitation were generated (924 permutations in total).

For each permutation, each vital rate was calculated for the LP and the MP treatment, and the difference between predictability treatments ($x_{LP} - x_{MP}$) was calculated, rendering the exact distribution of treatment differences. On the basis of this distribution, we then determined for each vital rate whether the observed treatment difference was significantly different from the expected treatment differences, assuming a two-tailed test with a significance level of $P < .05$. All analyses were run using R 3.5.0 (R Development Core Team 2018).

Population Dynamics

To compare the population dynamics among the two precipitation predictability treatments, a periodic, stage-structured, female-based matrix model was parameterized for each predictability treatment (Caswell 2001). This model included a matrix for each season. The spring matrix M_{sp} projected the population from three spring stages (AD, AD1, and Y) to four summer stages (AD, AD1, Y, and J_E):

$$\begin{array}{c} \\ \mathbf{J_E} \\ \mathbf{Y} \\ \mathbf{AD1} \\ \mathbf{AD} \end{array} \begin{array}{c} \begin{array}{ccc} \mathbf{Y} & \mathbf{AD1} & \mathbf{AD} \end{array} \\ \begin{bmatrix} 0 & R_{AD1\_sp} & R_{AD1\_sp} \\ S_{Y\_sp} & 0 & 0 \\ 0 & S_{AD1\_sp} & 0 \\ 0 & 0 & S_{AD\_sp} \end{bmatrix} \end{array}.$$

The summer matrix M_{sm} projected the population from four summer stages (AD, AD1, Y, and J_E) to five winter stages (AD, AD1, Y, J_E, and J_L):

$$\begin{array}{c} \\ \mathbf{J_L} \\ \mathbf{J_E} \\ \mathbf{Y} \\ \mathbf{AD1} \\ \mathbf{AD} \end{array} \begin{array}{c} \begin{array}{cccc} \mathbf{J_E} & \mathbf{Y} & \mathbf{AD1} & \mathbf{AD} \end{array} \\ \begin{bmatrix} 0 & 0 & R_{AD1\_sm} & R_{AD1\_sm} \\ S_{J_E\_sm} & 0 & 0 & 0 \\ 0 & S_{Y\_sm} & 0 & 0 \\ 0 & 0 & S_{AD1\_sm} & 0 \\ 0 & 0 & 0 & S_{AD\_sm} \end{bmatrix} \end{array},$$

and the winter matrix M_{wt} projected the population from five winter stages (AD, AD1, Y, J_E, and J_L) to three spring stages (AD, AD1, and Y):

$$\begin{array}{c} \\ \mathbf{Y} \\ \mathbf{AD1} \\ \mathbf{AD} \end{array} \begin{array}{c} \begin{array}{ccccc} \mathbf{J_L} & \mathbf{J_E} & \mathbf{Y} & \mathbf{AD1} & \mathbf{AD} \end{array} \\ \begin{bmatrix} S_{J_L\_wt} & S_{J_E\_wt} & 0 & 0 & 0 \\ 0 & 0 & S_{Y\_wt} & 0 & 0 \\ 0 & 0 & 0 & S_{AD1\_wt} & S_{AD\_wt} \end{bmatrix} \end{array}.$$

The asymptotic population growth rate λ was estimated as the dominant eigenvalue of the population projection matrix. Means and 95% confidence intervals were estimated for λ using a parametric bootstrapping approach (Wisdom et al. 2000). The annual population projection matrix was calculated as

$$A = M_{wt} \times M_{sm} \times M_{sp}.$$

Elasticity analysis, a widely used prospective perturbation analysis, was used to measure the sensitivity of λ to a change in a given vital rate, based on the annual projection matrix (Caswell and Trevisan 1994). Lower-level elasticities for common lizard vital rates were calculated analytically using the chain rule (Caswell 2001):

$$\frac{x}{\lambda}\frac{\delta\lambda}{\delta x} = \frac{x}{\lambda}\sum_{ij}\frac{\delta\lambda}{\delta a_{ij}}\frac{\delta a_{ij}}{\delta x},$$

where a_{ij} is the matrix element in row i and column j and x is a lower-level parameter of survival or reproductive rate. The term $\delta\lambda/\delta a_{ij}$ is the matrix element sensitivity, whereas $\delta a_{ij}/\delta x$ is the partial derivative of a given matrix element with respect to the lower-level parameter x.

Using a fixed one-way life table response experiment, a commonly used retrospective perturbation analysis (Caswell 1989), we identified the demographic causes of differences in λ between the two predictability treatments. Using the matrix of the MP precipitation regime as a reference, the observed difference in asymptotic population growth rate between the MP and the LP precipitation regime ($\Delta\lambda$) was decomposed into contributions from each vital rate, according to

$$\Delta\lambda = \lambda_{LP} - \lambda_{MP} \approx \sum_{ij}(x_{LP} - x_{MP})\frac{\delta\lambda}{\delta x_{MP}},$$

where $x_{LP} - x_{MP}$ represents the difference between treatments of the lower level-parameters and $\delta\lambda/\delta x_{MP}$ represents the sensitivity of the lower-level parameters, estimated using the reference matrix.

Effects of Delayed and Advanced Maturity

Differences in environmental conditions may lead to differences in growth rate (e.g., San-Jose et al. 2016; Romero-Diaz et al. 2017) and thus differences in the age at first reproduction. To assess the influence of delayed and advanced maturity on asymptotic population growth rate (λ), the basic life cycle (fig. C2) was reparameterized. To simulate a delay of maturity by 1 year in the LP treatment, which means that the first reproduction happens in the third instead of the second spring, we set R_{AD1_sp} and R_{AD1_sm} to zero in the matrix model for LP (fig. 1). To simulate an advance of maturity by 1 year—that is, first reproduction in the first instead of the second spring—we assumed that already yearlings reproduce by parametrizing R_{Y_sp} and R_{Y_sm} with the reproductive rates of the first-year adults of the basic model (R_{AD1_sp} and R_{AD1_sm}; fig. C2); likewise, R_{AD1_sp} and R_{AD1_sm} were equal to those of R_{AD_sp} and R_{AD_sm} of the basic model. All the rest

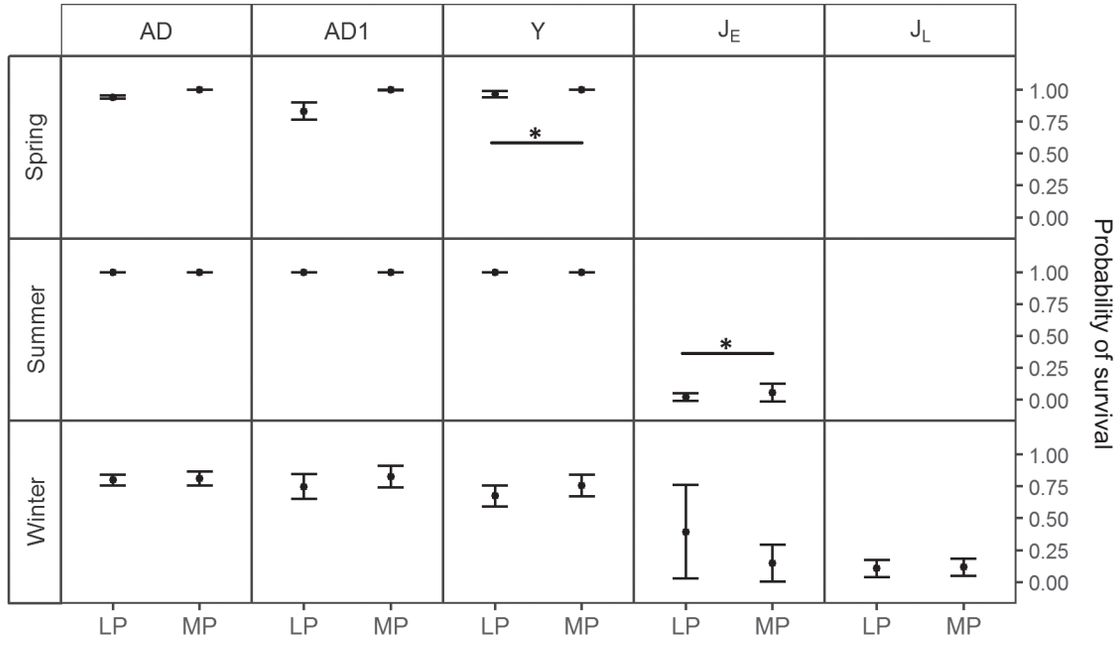

Figure 1: Survival probability (S) per season and age class, predicted by the mixed models for the less predictable (LP) and the more predictable (MP) precipitation treatment (means ± SE). Horizontal lines indicate significant differences in average survival among treatments, and asterisks indicate $P < .05$. Abbreviations: AD = adults; AD1 = first-year adults; Y = yearlings; J_E = early juveniles; J_L = late juveniles.

remained equal. For each model, we estimated the asymptotic population growth rate λ for the LP treatment, compared it with the previously derived λ for the MP treatment, and performed a prospective perturbation analysis. The R code of the above described models is available upon request.

Results

Spring survival of yearlings (S_{Y_sp}) and summer survival of early juveniles (S_{JE_sm}) were significantly higher in the MP compared with the LP treatment (fig. 1). In all other survival rates, differences among treatment levels were not significant (all $P > .05$; fig. 1). Survival was estimated for three seasons, five age classes, and a total of 12 combinations (fig. 1). In eight of the 12 combinations, lizards exposed to the MP treatment tended to exhibit higher survival (in the three spring measures, in four of five winter measures, and in one summer measure; note that in six of them, the difference was not significant). In contrast, winter survival tended to be higher in early juveniles (S_{JE_wt}) exposed to the LP treatment, and no visible differences existed in summer survival of adults (S_{AD_sm}), first-year adults (S_{AD1_sm}), and yearlings (S_{Y_sm}; fig. 1). There existed significantly more combinations where survival tended to be higher in the MP treatment ($t_{11} = 3.023$, $P = .012$; see app. A). Four reproductive traits were estimated for two seasons, two age classes, and 16 combinations, and there were no significant treatment differences (fig. 2). In seven combinations, reproductive parameters tended to be higher in the LP treatment; in another five combinations, reproductive parameters tended to be higher in the MP treatment; and no visible trends existed in the remaining four combinations (fig. 2). The frequency of the trend directions did not significantly differ from random expectation ($t_{15} = -0.565$, $P = .581$; app. A).

The asymptotic population growth rate ($\lambda < 1$) was significantly higher in the MP than in the LP treatment (fig. 3). The elasticity of λ to vital rates was most affected by changes in adult survival (S_{AD}), while changes in first-year adult (S_{AD1}), yearling (S_Y), and juvenile survival (S_{JE}, S_{JL}) exhibited small elasticities (fig. 4). Elasticities were almost identical between precipitation predictability treatments, and only in summer survival of early juveniles (S_{JE_sm}) were they higher in the LP treatment (fig. 4). The contribution of survival trends to differences in λ was highest for adult survival in spring (S_{AD_sp}) followed by adult survival in winter (S_{AD_wt}), and the contribution of the other survival trends was neglectably small (fig. 4). Elasticities of λ to reproductive rates were small (fig. 5). In adults, hatching success (H) at the end of spring and female ratio (F) at the end of spring exhibited the highest elasticities, and they were higher in the LP treatment (fig. 5). The contribution of differences in vital rates to differences in λ was neglectably small for most reproductive rates (fig. 5).

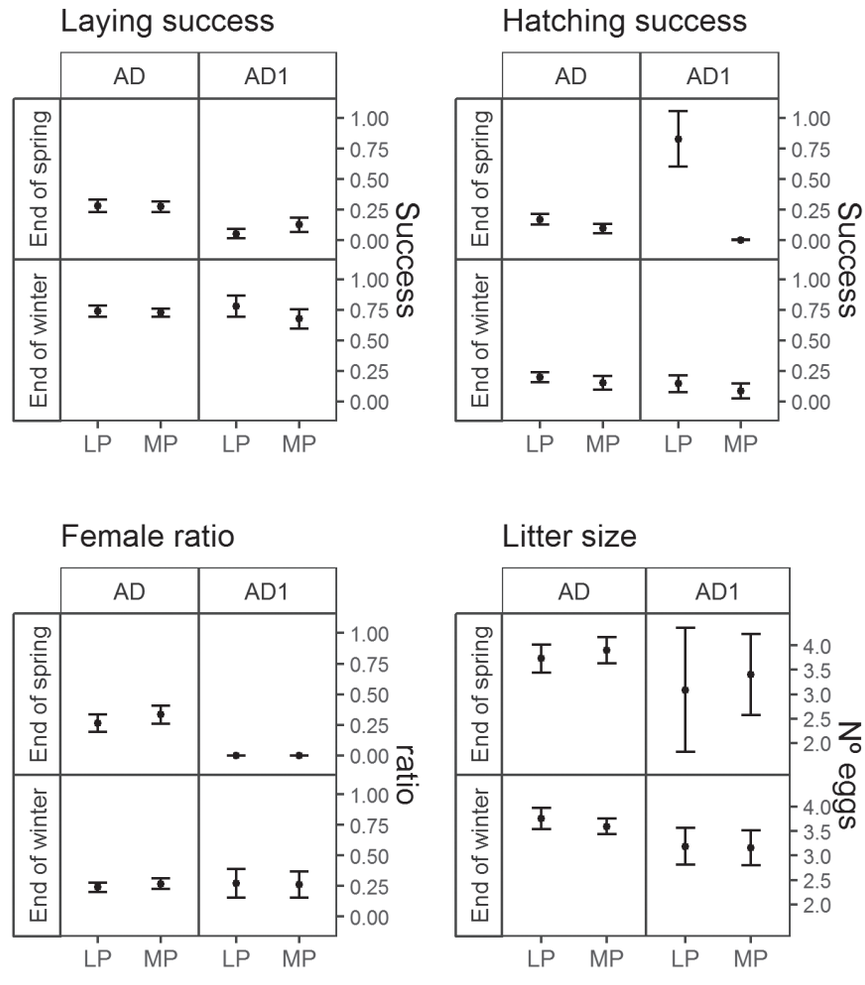

Figure 2: Reproductive rates for adult (AD) and first-year adult (AD1) females per season, predicted by mixed models for the less predictable (LP) and the more predictable (MP) precipitation treatment. Means ± SE are given. There were no significant differences in reproductive rates among treatments (all $P > .05$).

Delaying or advancing maturity by 1 year did not substantially affect population dynamics. In both models, asymptotic population growth rates were identical to those of the main model. In addition, in both model types perturbation analysis showed that the main contributors to λ were adult survival rates in spring and winter (S_{AD_sp}, S_{AD_wt}), as found in the basic model.

Discussion

Climate change scenarios forecast a reduction in the predictability of precipitation (IPCC 2013), and analyses over the past decades showed that the predictability of precipitation decreased over time while the probability of extreme precipitation events increased (IPCC 2013). Understanding whether and how such changes affect organisms is central for conservation, evolution, and ecology (Chevin et al. 2010). However, population responses to a decrease in predictability remain poorly investigated (e.g., Bjørnstad et al. 2004; Ashander et al. 2016), and to our knowledge, experimental proof is lacking. Here, we experimentally manipulated intrinsic precipitation predictability and tested its effect on the population dynamics of a short-lived lizard, the European common lizard *Zootoca vivipara*, using a seasonal stage-structured matrix model.

Experimental manipulation of precipitation predictability demonstrated that the simulated moderate decrease in precipitation predictability reduced the asymptotic population growth rate λ (fig. 3), in line with prediction 4. This result was robust with respect to treatment-induced differences in the age of first reproduction, since delayed and advanced maturity in LP led to the same treatment differences in λ as those of the standard life cycles. Significant treatment differences in spring survival of yearlings and summer survival of early juveniles as well as the significantly more frequent season ×

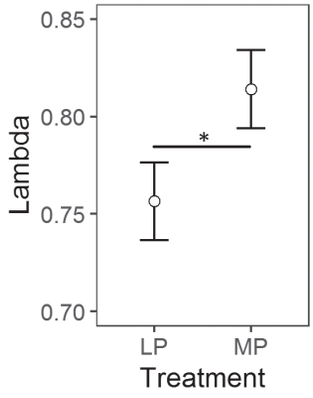

Figure 3: Asymptotic population growth rate λ in less predictable (LP) and more predictable (MP) environments. Shown are predicted means $\pm$ SE, and the asterisk indicates $P < .05$.

age class combinations with higher survival trends in the MP treatment (fig. 1) were in line with the observed decline in population growth rate (fig. 3). The elasticity and the prospective perturbation analyses showed that treatment differences in spring and winter survival of adults (fig. 4, *bottom*) mainly contributed to the decrease in population growth observed in the LP treatment (fig. 3). Although other survival probabilities varied between precipitation predictability treatments, their effect on population growth rate was almost null (figs. 1, 4). For example, yearling spring survival and summer survival of early juveniles were significantly higher in the MP treatment (fig. 1). The elasticity of λ to these parameters was low, and differences in elasticity among treatments were visible only in early juveniles (fig. 4, *top*), and their contribution to λ was negligible (fig. 4, *bottom*).

These results are in line with prediction 1, that survival may be negatively affected by decreased predictability (Durant et al. 2003; Jenouvrier et al. 2003; Sandvik et al. 2005; Lawson et al. 2015; Ashander et al. 2016). In our study, most treatment effects on survival were nonsignificant and existed mainly in spring and winter. However, the direction of the treatment effect was consistent (fig. 4), and the prospective perturbation analyses underpin the hypothesis that climatic predictability affects the survival rate of adults (Durant et al. 2003; Jenouvrier et al. 2003; Sandvik et al. 2005). Furthermore, significant negative effects found in juvenile (S_J) and yearling survival (S_Y) in the LP treatment but not in the hierarchically superior age classes (in juveniles: yearlings, AD1, and AD; in yearlings: AD1 and AD) are in line with prediction 3, that the precipitation predictability's effect may be stronger in the competitively inferior age classes (Grenot et al. 1987; San-Jose et al. 2016; Romero-Diaz et al. 2017) potentially because of inter–age class resource competition previous to hibernation (San-Jose et al. 2016). Similarly, the higher survival of adults and yearlings during the winter period (i.e., during early spring) in the MP treatment may have led to stronger inter–age class competition during sexual selection (San-Jose et al. 2016), potentially explaining the reduced survival of early

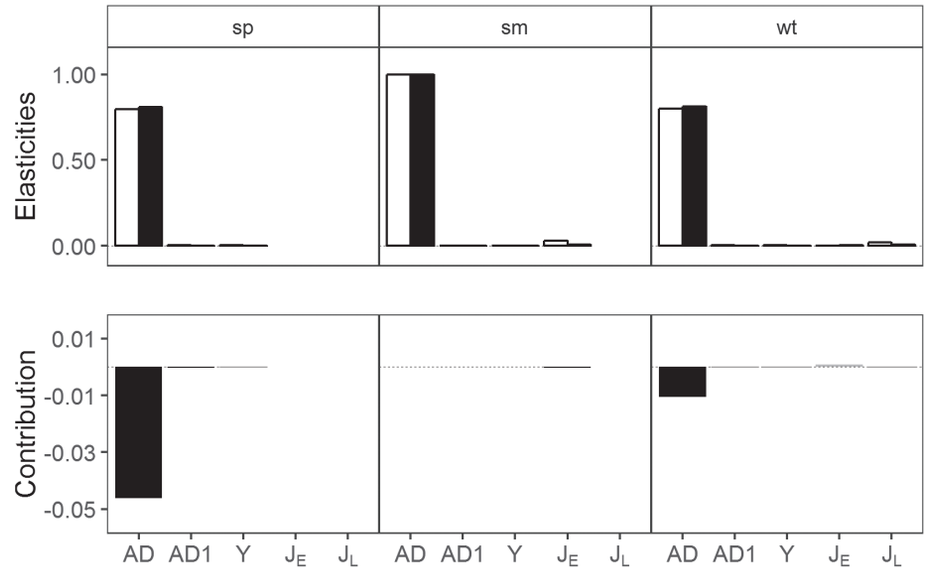

Figure 4: Elasticity of λ to survival (S; *top*) and the contribution of survival difference to the difference in λ (*bottom*) between less predictable (LP) and more predictable (MP) precipitation. For elasticity of λ, white bars depict the LP treatment, and black bars depict the MP treatment. For contributions, black bars depict situations where survival in the LP treatment is smaller than in the MP treatment, and gray bars depict situations where survival in the LP treatment is greater than in the MP treatment. Abbreviations: AD = adults; AD1 = first-year adults; Y = yearlings; J_E = early juveniles; J_L = late juveniles; sp = spring; sm = summer; wt = winter.

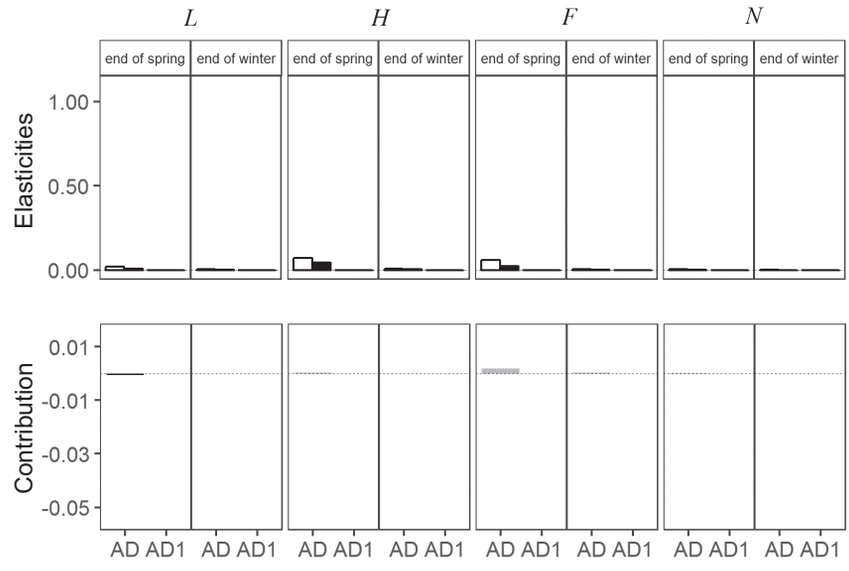

Figure 5: Elasticity of λ to vital rates (*top*) and contribution of the difference observed in vital rates to the difference in λ between the more predictable (MP) and the less predictable (LP) precipitation treatment (*bottom*). For elasticity of λ, white bars depict the LP precipitation treatment, and black bars depict the MP precipitation treatment. For contributions, black bars depict situations where vital rates in the LP treatment are smaller than in the MP treatment, and gray bars depict situations where vital rates in the LP treatment are greater than in the MP treatment. Abbreviations: AD = adults; AD1 = first-year adults; L = laying success; H = hatching success; F = female ratio; N = number of eggs.

juveniles (fig. 1). Thus, these effects on survival are in line with predictions from cohort resonance (Bjørnstad et al. 1999, 2004).

In contrast, reproductive rates were not affected by treatment, nonsignificant differences among treatments that may explain the observed decline in population growth rate were not consistent (fig. 2), and their contribution to differences in population growth was insignificant (fig. 5). These results contrast with prediction 2, that environmental predictability affects reproduction (Einum and Fleming 2004; Dewar and Richard 2007; Botero et al. 2015). Given that summer survival and the subsequent overwinter survival did not differ among treatments (overwinter survival: all $P > .3$; fig. 1), these results also suggest that the here simulated differences in precipitation predictability did not affect the trade-off between investing in reproduction and subsequent survival (under the trade-off, we would predict increased investment into reproduction during spring leading to reduced survival during summer and/or winter; Stearns 1992). This suggests that surviving individuals can cope with decreased predictability (Ashander et al. 2016) and that nonsignificant treatment differences in survival affected λ. The difference in λ between predictability treatments was in the range of 5.7% (fig. 3), showing that population decline was faster in LP environments, and with similar differences in subsequent years, populations exposed to less compared with the MP precipitation will decline more than 50% over 12 years. Moreover, life-history theory states that individuals should reduce reproductive investment and increase survival to reduce the deleterious effects of reduced predictability (Roff et al. 2002; Nevoux et al. 2010). However, *Z. vivipara* did not adjust reproduction, suggesting that changes in life-history strategy with respect to environmental predictability may be slow or absent (Ashander et al. 2016). Alternatively, treatment effects on reproduction may have been absent because during the last part of gravidity and during egg incubation, mothers and embryos were not exposed to the treatment.

Population growth was smaller than 1 in both predictability treatments (fig. 3) because of low reproductive output; for example, hatching success was on average around 20% (fig. 2). In our study, the contribution of treatment differences in reproduction to λ was almost zero (fig. 5). Since conditions experienced during gestation (in oviparous *Z. vivipara* during late gestation and egg incubation) were an important determinant of λ in an earlier study (Le Galliard et al. 2010), low reproductive output and nonexposure of eggs and mothers during late gestation may have hindered detecting treatment effects on reproduction; thus, our results most likely reflect a conservative estimate of how precipitation predictability affects λ.

The precipitation predictability effect on λ is particularly dramatic since in our population experiment adult survival—the main contributor to the difference in λ—is almost twice as high as in the natural populations (average

annual adult survival, S_{AD}: 0.45 ± 0.15 SE in the Pyrenees [Heulin et al. 2011], 0.42 ± 0.06 SE in the Cévennes [Massot et al. 2011], 0.81 ± 0.06 SE in populations exposed to MP precipitation). This finding experimentally underpins the results of theoretic studies predicting that LP environments will increase the risk of population extinction (Chevin et al. 2010; Ashander et al. 2016).

In summary, our results experimentally show that the predicted decrease in an environment's predictability (IPCC 2013) could exacerbate the rate of currently observed population decline and extinction (e.g., 12% of extinction since 1975 in lizards; 48% of rapidly declining amphibian species; 21% of bird species are extinction prone and 6.5% functionally extinct; Şekercioğlu et al. 2004; Sinervo et al. 2010). The important effects of the nonsignificant survival differences on λ show that even nonsignificant and small effects can have major consequences (Bjørnstad et al. 2004) and that those may not be anticipated by studies of short duration and studies analyzing a few parameters. On the contrary, only the here applied stage-structured matrix model allowed us to understand the consequences of differences in precipitation predictability on population dynamics, while a few selected parameters measured in 1 or 2 years on the individual level would not have led to the same conclusions (see app. B; apps. A, B are available online). Consequently, assessment of how changes in an environment's predictability affect populations, species' persistence, and biodiversity requires solid and difficult to obtain data that allow testing effects on the population dynamics using stage-structured matrix models, since only those models may allow us to understand the ultimate effects of changes in environmental predictability.

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APPENDIX A

Calculation of the *t* Statistics for the Trends Observed in Vital Rates

To test whether the nonsignificant trends in vital rates (fig. 1) consistently exhibit the same direction, the different trends were parametrized as follows: if a vital rate tended to be higher in the MP treatment (i.e., if a tendency was visible by eye in fig. 1), it was given a value of 1; if no differences were observed between treatments, a value of 0 was given; and if the vital rate tended to be higher in the LP treatment, a value of -1 was given. Thereafter, a one-sample test based on the *t* statistics was performed with the null hypothesis that no consistent trend existed; that is, mean $= 0$. This test reflects a conservative statistical model for testing whether the directions of the treatment effect deviate from random expectation. Also note that Wilcoxon signed-rank tests rendered the qualitatively same results.

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